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A four-legged snake from the Early Cretaceous of Gondwana

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Snakes are a remarkably diverse and successful group today, but their evolutionary origins are obscure. The discovery of snakes with legs has shed light on the transition from lizards to snakes, but no snake has been described with four limbs. We describe a four-limbed snake from the Early Cretaceous (Aptian) Crato Formation of Brazil. The new snake has a serpentiform body plan with an elongate trunk, short tail, and large ventral scales suggesting characteristic serpentine locomotion, but retains small, prehensile limbs. Furthermore, the body proportions and reduced neural spines indicate a fossorial lifestyle, suggesting that snakes evolved from burrowing rather than marine ancestors. The structure of the hind limbs suggests that they may have functioned either to grasp prey or as claspers during mating. Hooked teeth, an intramandibular joint, a flexible spine capable of constricting prey, and the presence of vertebrate remains in the guts indicate that this species preyed on vertebrates, and that snakes made the transition to carnivory early in their history. Together with a diverse fauna of basal snakes from the Cretaceous of South America, Africa, and India, the new snake shows that crown Serpentes originated in Gondwana.

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Snakes are among the most diverse groups of tetrapods, with >3,000 extant species exploiting a remarkable range of niches(1). Snakes inhabit deserts and rainforests, mountains and oceans, and despite lacking limbs, employ an extraordinary range of locomotor styles, including crawling, burrowing, climbing, swimming, and even gliding(1). All snakes are predators, but they consume a wide range of prey, from insects to large mammals (1). This diversity is made possible by a specialized body plan, which includes an elongate body with reduced limbs, a kinetic skull and ribs to swallow large prey(2), and a specialized forked tongue and vomeronasal organ to detect chemical gradients(1). The origins of this body plan remain unclear, however(1). New fossils(2-5), including snakes with large hindlimbs(6, 7) have shed light on the lizard-snake transition, but no snake has been reported with four limbs. Here, we report a new fossil snake from the Early Cretaceous of Gondwana that exhibits the primitive tetrapod condition.

Reptilia Laurenti, 1768
Squamata Oppel, 1811
Ophidia Latreille, 1804
Tetrapodophis amplectus gen. et sp. nov.

Etymology. Greek *tetra*, ‘four’, *pod*, ‘foot’ and *ophis*, ‘snake’; Latin *amplectus*, embrace.

Holotype. BMMS (Museum Solnhofen) BK 2-2

Locality and horizon. Nova Olinda Member of the Crato Formation (Early Cretaceous: Aptian), Ceará, Brazil(8).

Diagnosis. 160 precaudal and 112 caudal vertebrae, short neural spines, four limbs, metapodials short; penultimate phalanges hyper-elongate and curved, phalangeal formula 2?-3-3-3-3? (manus) 2-3-3-3-3 (pes).

Description. The skeleton and associated soft tissues are preserved on laminated limestone as part and counterpart (Fig. 1). The skull (Fig. 2) has a short rostrum and long postorbital region, as typical of snakes. The premaxilla is short and tall, with at least two teeth. The left maxilla shows a tall facial process, which rises up steeply, as in *Coniophis*. Frontals, parietals and nasals are smooth dorsally, as in other snakes. The L-shaped nasal resembles *Dinilysia* (9) and Simoliophiidae(10) in being tall and narrow between the

caudally extended external nares, and transversely expanded to form a hinge with the frontals. A bony plate below the parietal probably represents the parietal ventral wing.

The dentary is snake-like, being long and bowed. The subdental ridge is deep anteriorly, as in other snakes, but shallow posteriorly, as in *Coniophis*(2), *Dinilysia*(9), and *Najash*(11). As in other snakes(9), the splenial contacts the subdental ridge posteriorly but not anteriorly, and lacks an anterior inferior alveolar foramen. Posteriorly it tapers and forms a concave joint with the angular, indicating the existence of an intramandibular hinge.

Maxillary and dentary teeth are typical of snakes, being expanded basally with long, slender crowns that hook posteriorly. Implantation is sub-acrodont, and interdental ridges, a snake feature(12), are present. Replacement teeth are horizontally oriented, another snake synapomorphy(12, 13).

There are 160 precaudal vertebrae; among squamates, only snakes have >150 precaudal segments(13). The trunk (Figs. 1, 3) coils anteriorly, then forms a sinuous curve before the spine curves sharply near the middle of the series. This extreme flexibility is unique to snakes among squamates.

As in other snakes, trunk vertebrae are uniform. Neural arches are low, broad, and inflated. Extensive overlap between adjacent arches and the inflation of the neural arches indicate development of the ophidian zygosphenes-zygantrum articulation. Neural spines are short, as in other early snakes (2, 11) and posterodorsally directed, as in *Najash*(11). Neural spines lie just ahead of the posterior margin of the neural arch, such that the posterior margin of the arch would be gently V-shaped, as in *Coniophis*(2). Neural arches bear posterolateral tuberosities, as in *Coniophis*(2) and *Dinilysia*(14).

Synapophyses have a kidney-shaped articular surface. The distinct hemispherical condyle and planar cotyle of alethinophidians is absent; the articular surface is gently convex, as in lizards and basal snakes(2). As in other squamates(13), centra are procoelous. Ventrally, centra bear a low, rounded haemal keel, paired subcentral foramina, and subcentral ridges extending posteriorly from the synapophyses to define subcentral lymphatic fossae. Paired subcentral foramina are present.

The single-headed ribs articulate with synapophyses low on the centrum. Tubercular processes, a snake apomorphy, are absent anteriorly but prominent in mid-posterior segments. Ribs are strongly curved proximally but lack the strong distal curvature of crown snakes, and are gently bowed, as in *Najash*(11).

The two sacral vertebrae bear short, stout ribs, as in *Najash*(11). There are 5-6 cloacal vertebrae, with a lymphapophysis on segment 160. There are 112 caudals. Anterior caudals bear short ribs; these are anterolaterally directed, as in *Najash*(11) and Simoliophiidae(10). The tail is short (~38% of trunk length) as in other snakes and burrowing squamates(15).

No pectoral girdle is visible. The humerus (Fig. 4) is rodlike with a rudimentary deltopectoral crest, and lacks the entepicondyle and ectepicondyle. The antebrachium is short, with a robust radius and slender ulna; both bowed posteriorly. A radiale is present; the other carpals are unossified. The manus phalangeal formula is 2?-3-3-3-3. Metacarpals are short and broad, with a stout metacarpal I and block-like metacarpals II-IV. Phalanx I-1 is preserved as a mould. Proximal phalanges of II-IV are slightly longer than the metacarpals; penultimate phalanges are hyperelongate. Short, curved unguals are present.

The pelvis (Fig. 4) resembles that of *Najash*. The ilium's postacetabular process is a thin, gently curved bar, as in *Najash*(11) and Simoliophiidae(16). Femora are short and robust, as in *Najash*(11). They differ from *Najash* but resemble Simoliophiidae in having a straight shaft. The flat proximal end suggests unossified epiphyses, making the specimen a juvenile or hatchling. The trochanter is small and proximally positioned compared to *Najash* (11). The tibia is short, straight, and robust; the fibula is bowed as in simoliophiids (16) and *Najash* (11). A large astragalus and small calcaneum are present; distal tarsals are unossified.

Metatarsals are abbreviated and robust. MT I is twice as long as wide; MT II-IV are more slender and about 60% as long as MT I. MT V is broad, and hooked as in other squamates (13). The phalangeal formula is 2-3-3-3-3, as for the manus. I-1 is elongate and moderately robust. The shape and proportions of the phalanges resemble those of the manus.

Soft tissue preservation. Faint impressions of scales, representing the transverse ventral scales, occur ventrally. Approximately 30 tracheal rings are preserved between vertebrae 10-21 (Fig. 4B). and a trace of the oesophagus is seen adjacent to the trachea. In the posterior abdomen (Fig. 4A), instestinal contents preserve as a pinkish-brown, fine grained phosphatic material containing long bones of a small tetrapod, perhaps a squamate or anuran.

Systematics. Numerous synapomorphies and autapomorphies (* = ophidian autapomorphy) make the snake affinities of *Tetrapodophis* unambiguous. These include L-shaped nasals*; nasal descending lamina; unicuspid, hooked* teeth; horizontal replacement teeth*; subacrodont implantation; interdental ridges; a deep subdental ridge; trunk elongation; zygosphenes-zygantrum articulations; an arched neural arch with posterolateral mounds*; short neural spines; haemal keels*; large subcentral fossae/foramina, tubercular processes of the ribs*; lymphapophyses*; a long, slender ilium, limb reduction, transverse ventral scales*; and a feeding strategy where large prey are ingested whole. While some of these features occur in other squamates, snakes are the only group to exhibit all of them, and many of these characters are uniquely ophidian.

To test *Tetrapodophis*' ophidian affinities we used a morphological matrix(13, 17) to conduct four phylogenetic analyses: with and without molecular backbone constraint(18), and with equal and implied weighting(19). In each analysis, *Tetrapodophis* emerges as a basal snake. *Tetrapodophis* emerges as sister to *Coniophis* when a molecular backbone is used (Fig. 5), otherwise its position relative to *Coniophis* and *Najash* is unresolved. With toxicoferan monophyly enforced, snakes emerge as sister to the Mosasauria, i.e. Pythonomorpha.

Discussion. As the only known four-legged snake, *Tetrapodophis* elucidates the evolution of snakes from lizards. While retaining four limbs, the forelimbs are smaller than the hindlimbs, foreshadowing their loss in *Najash* and later snakes. Phalanges are lost from both the manus and pes. Reduction in the number of phalanges is common among long-

bodied squamates(20), but the digital formula seen in *Tetrapodophis* is unique. Both forelimbs and hindlimbs appear to be functional in *Tetrapodophis* but their function is unclear. The abbreviated proximal phalanges, slender and hyperelongate distal phalanges, and isodactyly recall the prehensile feet of animals such as scansorial birds, sloths(21) and bats, suggesting a grasping function. Conceivably, the limbs could have functioned for grasping prey, or mates. Regardless, *Tetrapodophis* shows that after the initial evolution of serpentine locomotion, the limbs were repurposed for a grasping function.

The origins of the snake body plan are controversial. Snakes are variously interpreted as evolving from either burrowing(2, 6, 7) or marine(16) ancestors. *Tetrapodophis* lacks aquatic adaptations (e.g. pachyostosis, laterally compressed tail) and instead exhibits features of fossorial snakes and other burrowing squamates: a short rostrum and elongation of the postorbital skull, trunk elongation, a shortened tail(15, 22), short neural spines(11), and reduced limbs(15, 22). Along with similar adaptations in *Najash*(6, 11) and *Coniophis*(2), *Tetrapodophis* suggests derivation of snakes from burrowing lizards. Marine habits in Mosasauria and Simoliophiidae are best interpreted as derived, rather than plesiomorphic.

Tetrapodophis also exhibits a suite of predatory adaptations. These include recurved, claw-like teeth to seize large prey, a highly flexible spine (>150 precaudal vertebrae) allowing the body to be coiled around prey, and an intramandibular joint, facilitating ingestion of large prey. These features— and the presence of a vertebrate in the gut— show that *Tetrapodophis* preyed on vertebrates. Similar adaptations occur in other early snakes(2, 9). Although insectivory has previously been proposed to be primitive for snakes (1) these adaptations show that snakes made the transition to carnivory early in their history.

Finally, *Tetrapodophis* sheds light on snake biogeography. The center of toxicoferan diversification is Laurasia, with the oldest Anguimorpha and Iguania(13) first appearing there. The existence of *Tetrapodophis* in the Aptian of Gondwana, however, along with the existence of basal snakes in the Cretaceous of South America(11, 14), India(23), Madagascar(24) and Africa(25), as well as Tropidophiidae and Aniliidae in

South America(1), supports the hypothesis that Serpentes initially radiated in Gondwana(1).

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26. DM, NRL and HT designed and performed research; NRL performed the phylogenetic analysis, DM and NRL wrote the paper.

Supporting Online Material

Figs S1-S7, Table S1

SOM Text

Character-taxon matrix

Constraint tree

Figures + Figure Captions



Figure 1 | *Tetrapodophis amplexus*, holotype part and counterpart. a, counterpart, showing skull and skeleton impression; **b**, main slab, showing skeleton and skull impression.

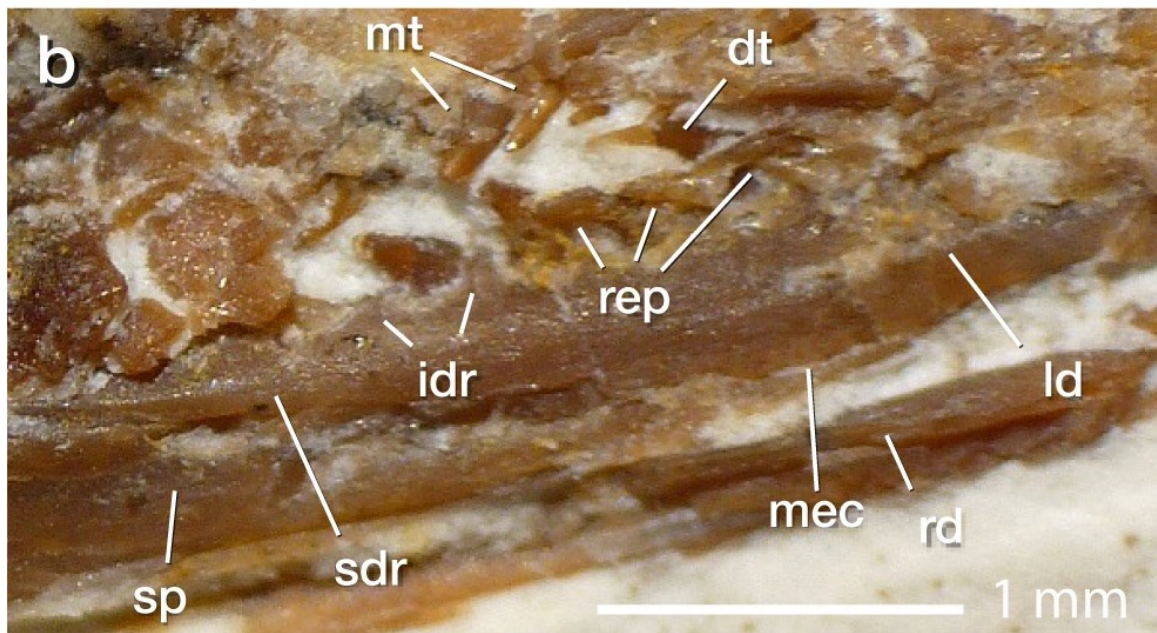
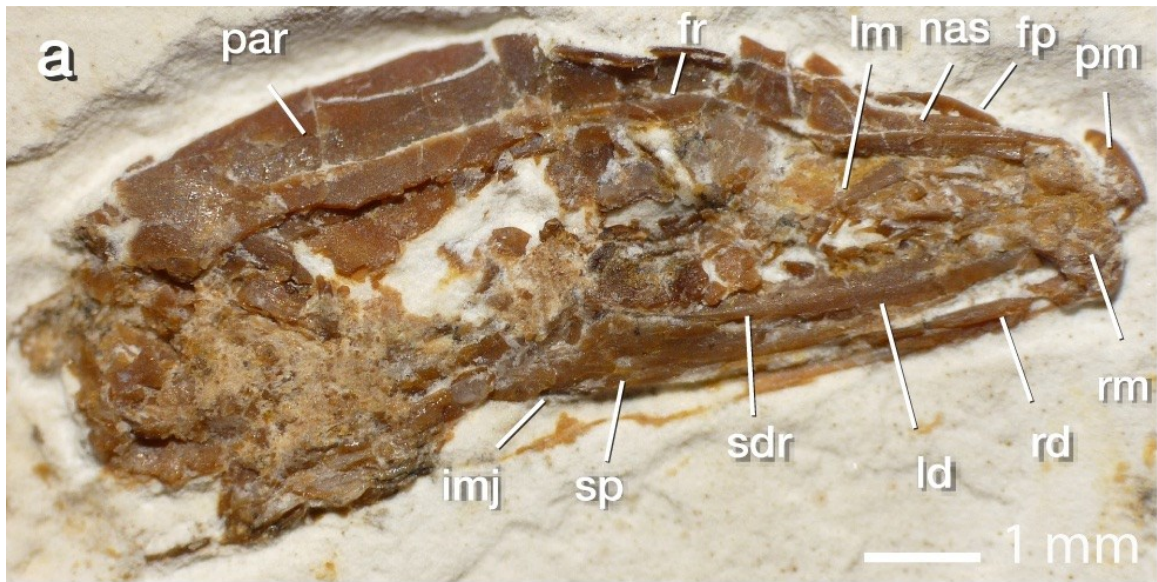


Figure 2 | *Tetrapodophis amplexus*, skull and left mandible. a, skull; **b**, left mandible in medial view. Abbreviations: dt, dentary tooth; fp, facial process of maxilla, fr, frontal; lm, left maxilla, ld, left dentary; mt, maxillary teeth; nas, nasal, par, parietal; pm, premaxilla; rd, right dentary; rd, right dentary; rt, replacement teeth; sdr, subdental ridge; sp, splenial.

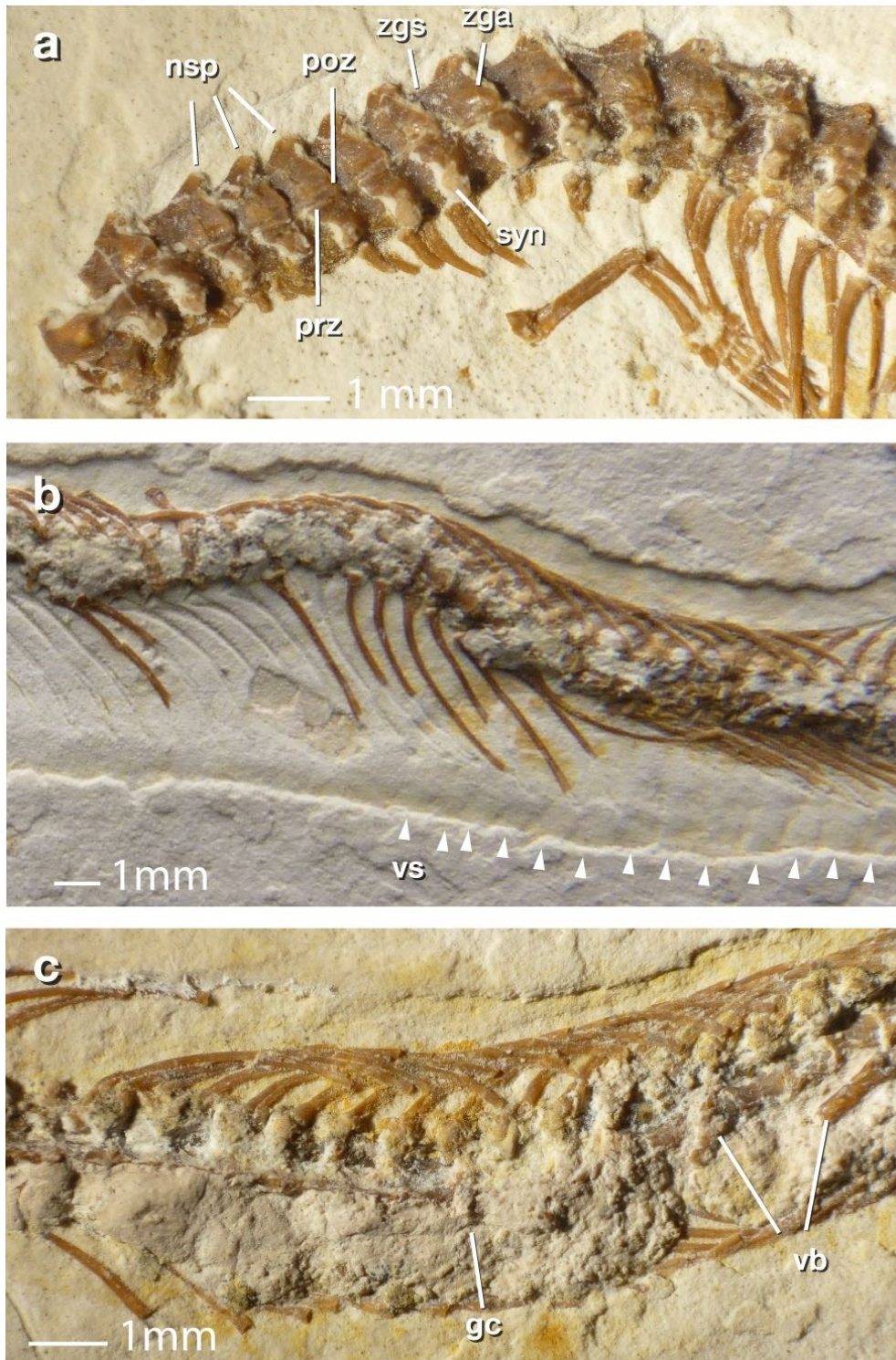


Figure 3 | *Tetrapodophis amplexus* axial column. a, cervicals and anterior presacrals; **b**, mid-thorax, showing ventral scale impressions; **c**, posterior thorax, showing gut contents and bones of prey. Abbreviations: gc, gut contents; nsp, neural spines; poz, postzygapophysis; prz, prezygapophysis; vb, vertebra bone; vs, ventral scales; zga, zygantrum; zgs, zygosphene.

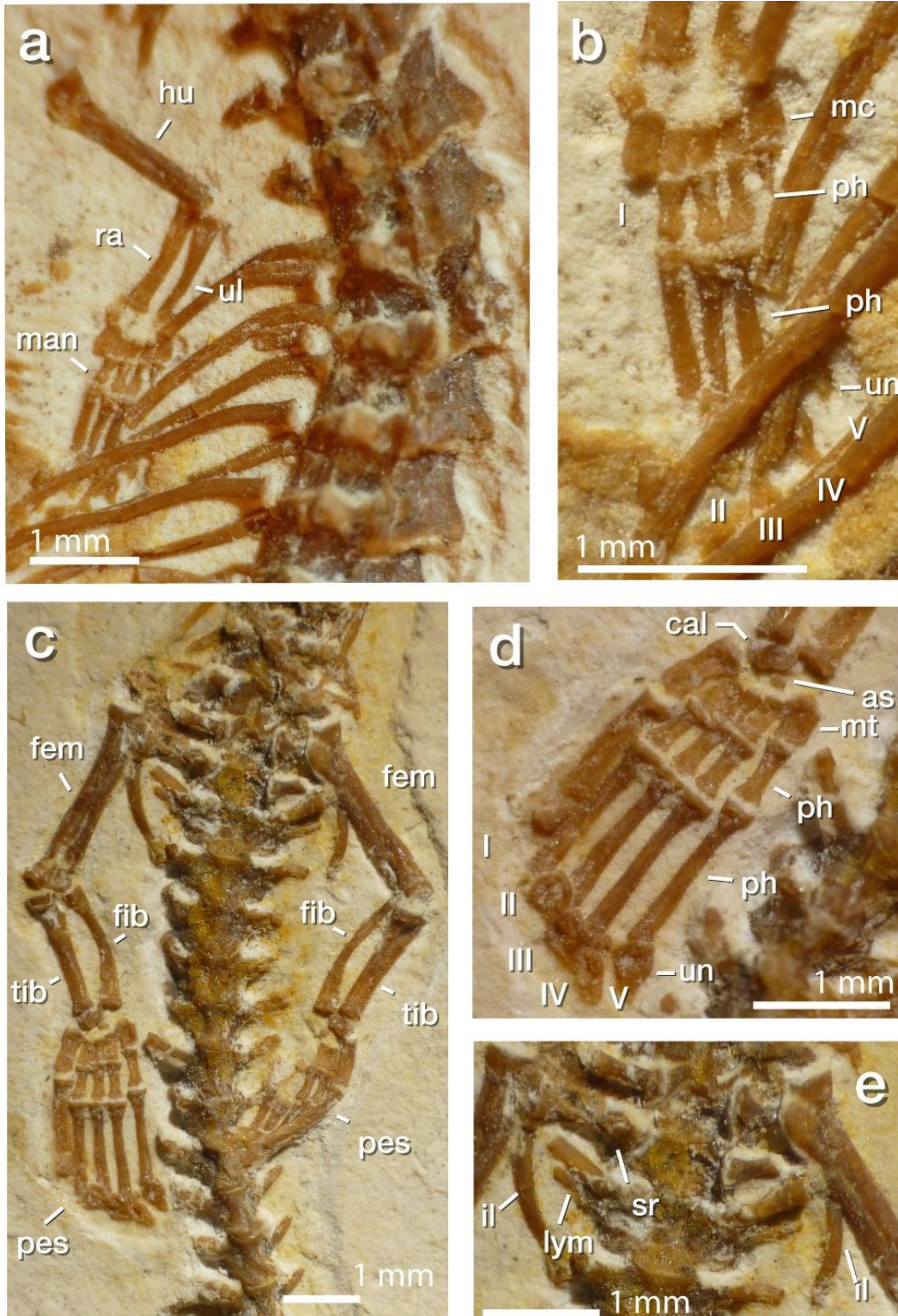


Figure 4 | *Tetrapodophis amplexus* appendicular morphology. a, forelimb; b, manus, c, hindlimbs and pelvis, d, pes, e, pelvis. Abbreviations: fem, femur; fib, fibula; hu, humerus; il, ilium; lym, lymphapophysis; ma, manus; mc, metacarpal; mt, metatarsals; ph, phalanges; ra, radius; sr, sacral rib; tib, tibia; ul, ulna; un, ungual.

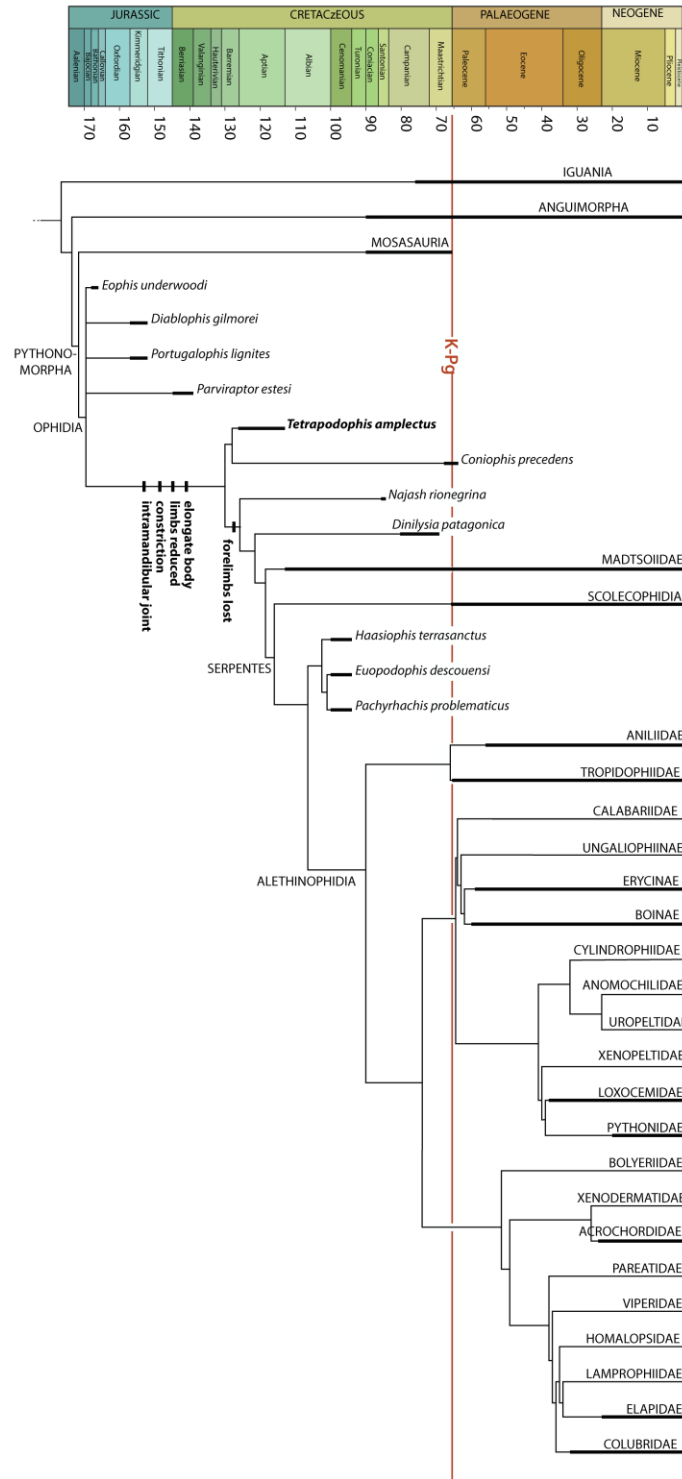


Figure 5 | Phylogenetic position of *Tetrapodophis*. Strict consensus of 85 most parsimonious trees found using implied weights and a molecular constraint (see SI for full details) for a matrix of 632 characters and 205 taxa.